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Breeding limits foraging time: evidence of interrupted foraging response from body mass variation in a tropical environment

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Abstract

Birds should store body reserves if starvation risk is anticipated; this is known as an 'interrupted foraging response'. If foraging remains unrestricted, however, body mass should remain low to limit the predation risk that gaining and carrying body reserves entails. In temperate environments mass gain in female birds during breeding is often attributed to egg formation and mass loss after incubation to flight adaptation or the effect of reproductive workload, rather than as a result of an adaptive interrupted foraging response to the limited foraging time or unpredictable foraging conditions that breeding demands. In tropical environments, foraging conditions vary more within the breeding season than in temperate environments, and so studies in tropical environments are more suited to decouple the potentially confounded effects of increase in body reserves versus egg formation on the body mass of breeding birds. In this study, we test whether breeding results in an interrupted foraging response in a tropical savannah system using body mass data collected over a 15-year period from female Common Bulbuls *Pycnonotus barbatus*. This species breeds both in the wet and dry season, despite fewer resources being available in the dry season. Breeding stage predicted female body mass: body mass peaked abruptly during incubation, but was not closely associated with the egg-laying stage, and declined during brood rearing. Breeding females were heavier in the dry season than in the wet season. In the dry season, heavier birds were more likely to incubate eggs or brood chicks. These observations suggest that increased body reserves are required to buffer the consequence of limited foraging time or impoverished foraging conditions, which may be most pronounced during incubation and in the dry season, respectively. Such mass increases are consistent with an interrupted foraging response, which may apply to temperate zone birds experiencing foraging restrictions during breeding.

Key words

Body reserves, breeding status, food availability, foraging unpredictability, reproduction, starvation-predation risk, tropical seasonal variation, tropical birds.

Introduction

Foraging time in breeding birds may be restricted by breeding roles, such as territoriality, mate guarding, nest building, incubation and brood rearing, as well as the constraints of having to forage in a central place and deliver food to a fixed nest site. As a consequence, breeding birds may carry extra body reserves to reduce the risk of starving due to limited foraging time or unpredictable foraging conditions, even though this may increase predation risk (Lima 1986; Gosler et al. 1995). This body mass gain strategy is called the 'interrupted foraging response' (Lima 1986; Macleod and Gosler 2006): unpredictable foraging leads to increase mass reserves whether this is, for example, shorter day length in winter or shorter available time to forage during the breeding season.

The interrupted foraging response may then provide a simple universal explanation for body reserves carried by breeding birds beyond the egg laying stage in addition to the unavoidable additional mass that increased size of reproductive organs and egg production entail. For example, body mass gained during breeding has been shown to correlate positively with adult survival probabilities in tropical savannah birds (Cox and Cresswell 2014), which suggests that body reserves carried during breeding decrease starvation risk and increase survival likelihood when foraging opportunities become relatively unpredictable for breeding birds. However, body reserves in birds should reflect a trade-off between their costs and benefits (see Witter & Cuthill 1993). Hence, if starvation risk is low, body mass should remain relatively low even during breeding to limit predation risk (Macleod et al. 2005; Macleod et al. 2008).

Differences in body reserves carried between breeding stages should reflect relative starvation risk between these stages or how available foraging time is constrained by each stage. For example, in the Blue Petrel *Halobaena caerulea*, body mass before and after incubation bouts, and food availability at sea during foraging may predict incubation duration and foraging bouts, likelihood of temporary egg neglect, rate of body mass gain during foraging and overall breeding success (Chaurand and Weimerskirch 1994). Within a breeding attempt, foraging time may be most limited during incubation because incubating birds have to spend a fixed amount of time on their eggs in order for them to develop and hatch as quickly as possible. Larger body reserves may then be particularly valuable if the foraging environment is relatively unpredictable during incubation because birds are less likely to obtain sufficient food in each foraging bout.

Body mass variation in breeding birds has received considerable attention in temperate environments compared with tropical ones. In temperate environments, body mass gain before incubation in female birds has been attributed to the increased size of reproductive organs (Vezina & Salvante 2010), while mass loss after or during incubation is attributed to the effect of reproductive workload or adaptation for better flight performance during nest provisioning (Merkle & Barclay 1996; Neto & Gosler 2010; Boyle, Winkler & Guglielmo 2012). Pre-incubation body mass gain due to increased size of reproductive organs is largely undisputed (see Vezina & Salvante 2010), but the reproductive stress and flight adaptation hypotheses have been tested using experimental food supplementation to temperate breeding birds (Moreno 1989; Merkle and Barclay 1996). However, body mass response to food supplementation in experimental set-ups may be uninformative if non-supplemented control breeding birds do not anticipate any foraging unpredictability. Experimental reduction of food may also be less practical in natural systems where birds move freely and can use other resources. An alternative approach, however, might be to model patterns of breeding

body mass from long-term data of individual birds ringed within the same environment with clear resource seasonality for bird species with protracted breeding periods.
Such data are available in a tropical savannah breeding environment for the Common Bulbuls *Pycnonotus barbatus*, which can breed throughout the year (see also Cox *et al.* 2013). By using brood patch presence and development as indicators of breeding occurrence and stage, respectively (Redfern, 2008; Redfern 2010), we assessed how body mass varied within the breeding period and between environmental conditions. The different stages of brood patch development are closely linked to breeding stages in European passerines (Redfern 2010; Myers & Redfern 2011). We assume that savannah bird species show a similar progression of brood-patch development (Table S1). We expect that body reserves will increase with breeding stages that constrain foraging such as incubation but with an interaction with availability of resources. For the Common Bulbuls, the dry season in a tropical savannah is expected to be less favourable for breeding than the wet season because insect abundance is low, and food and water are less widely distributed (Molokwu et al. 2008; Molokwu et al. 2010; Brandt and Cresswell 2008). The occurrence of moult may confound the effect of breeding on body mass variation (Gosler 1994) and, therefore, we also consider the possible confounding effects of moult here. We therefore expect that body reserves will offer a greater reproductive advantage under less favourable foraging conditions (Smith & Moore 2003), resulting in more pronounced body mass gain for breeding birds in the dry season in our study area. We, therefore, test two hypotheses:

1. Body mass within a breeding attempt varies in accordance with the level of foraging unpredictability at different breeding stages independently of mass gains due to egg formation. Foraging unpredictability is expected to peak during incubation.
2. Body mass during breeding varies seasonally with peaks in the dry season when foraging is expected to be most unpredictable.

Methods

Study site

Our study was carried out in Amurum Forest Reserve (09°52'N, 08°58'E), at the A.P. Leventis Ornithological Research Institute (APLORI), on the Jos Plateau in Nigeria. The Amurum Forest Reserve consists of four main habitat types: a regenerating savannah woodland, riparian forests, rocky outcrops (inselbergs) and farmlands. Much of the land surrounding the reserve, like the reserve itself before 2001, is degraded by anthropogenic pressure from farming, bush fires and livestock grazing. There is a single wet and dry season per year lasting about six months each. Generally, the wet season spans from May to mid-October while the dry season spans from the end of October to April. Total monthly rainfall is above 150mm in the wet season except for May and October when it may be lower, while there is almost entirely no rainfall in the dry season. Temperatures vary across the year: temperatures are lowest (8 - 14 ^{o}C) during the dry cold windy periods in December and January when relative humidity may be as low as 10% and also at the peak of the wet season in July and August; temperature maxima (28 - 32 ^{o}C) are in March and April before the start of the wet season (Cox *et al.* 2011; Figure S1).

Study species

The Common Bulbul is widespread throughout Africa. They are sexually monomorphic, usually 9 - 11 cm and weigh 25 - 50g. They have an annual survival probability of 0.67 ± 0.05 (Stevens *et al.* 2013), but some adults can live for up to 15 years in the wild. The Common Bulbul breeds in both the wet and the dry season in our study area with an average clutch size of two. Most breeding attempts fail due to nest predation. Nest

building takes 3 - 5 days, egg laying 2 - 3 days, incubation 13 - 14 days, and nestlings leave the nest at 12 days after hatching. Breeding roles are shared by parents. Females build the nest while being guarded by the males. Females incubate the eggs while the male perches close by until both go foraging between incubation bouts. Males feed nestlings during the early nestling phase while females brood chicks. Later, females feed nestlings while males guard the nest from a nearby perch. Both parents continue to feed chicks after fledging and Bulbuls may still remain in family groups for 12 weeks after the chicks have left the nest. Bulbuls moult almost exclusively in the wet season, although a few individuals may start before or at the end of the wet season depending on annual rainfall variability. Common Bulbuls are largely frugivorous but nestlings are predominantly fed insects. Adult birds may also occasionally feed on insects, nectar and seeds. Fruits are available to Bulbuls year round but from different fruit plants, which vary in fruiting phenology, so that food availability may be constrained by the distribution of a specific fruiting plant. Moreover, insect abundance peaks occur in the wet season while seeds are more readily available at the end of the wet season and start of the dry season.

Data collection and determination of variables

Birds were caught using mist nets from 06:00 to 10:30 hours between 2001 and 2015, inclusively. In the years 2001 and 2013, trapping was mostly concentrated at Constant Effort Sites (CES) during a CES ringing project, which takes place 5 times each year for six consecutive days each. During the CES, 272 meters of nets were used in total. In 2014 and 2015, in addition to the regular CES captures, trapping was carried out repeatedly throughout the entire year with variable lengths of mist nets in addition to the use of playback devices, depending on the trapping area covered.

We trapped 1,422 birds in total, and 271 individuals were trapped repeatedly a total of 673 times. From all birds trapped, there were 135 females with brood patches and 69 identified non-breeding female birds; 50 of these females were caught more than once but at least once with a brood patch. In total these 50 females were caught 147 times. Where possible, caught birds were aged and sexed by the presence of a gape and a brood patch, respectively.

Because only the sexes of breeding female Common Bulbuls are reliably determined by field observations, we considered only adult females for this study. Breeding status and stage were assessed on the basis of brood patch occurrence and development (Table S1). In addition, we verified the relationship between brood patch development and breeding stages in female Common Bulbuls that were caught raising young or incubating eggs. Also note that Common Bulbul females incubating or brooding chicks have a brood patch score of 3 while those feeding chicks may have a brood patch score of 3 or 4, depending on whether females are still brooding. We are confident that only female Common Bulbuls have brood patches and so birds can be sexed reliably based on brood patch occurrence; however, we verified the sexes of birds with brood patch score of 5 from our molecular sexing data because males undergoing moult may be erroneously scored as having a brood patch of 5.

For each trapped bird, we recorded wing length (± 1mm), moult status, pectoral muscle score, fat score, brood patch score and body mass (± 0.1g, Ohaus Scout). Moult was scored as present or absent: an individual actively replacing main wing or tail feathers was scored 1; otherwise, it was scored as 0 (Svensson 1991, Redfern and Clark, 2001). Birds were labelled as caught during the wet or dry season, based on the usual precipitation in the period when they were caught. The 16th of October to the 30th of April was considered to be dry season, while the 1st of May to the 15th of October was considered the wet season.

Statistical analyses

To test the hypothesis that breeding birds vary body mass in accordance with the level of foraging unpredictability at different breeding stages but controlling for the timing of mass gains due to egg formation, we built a General Linear Mixed Model (GLMM) with body mass as a response variable and brood patch score as a predictor. We controlled for the effect of body size and seasonal variability by including wing length and season of capture in the model, respectively. We also controlled for inter-annual and individual variability between capture years and individuals, respectively, by including year of capture and individual identity in the model as random factors. Individual identity did not significantly improve overall model fit (contribute any additional variance) and so was dropped from the final model.

To test the hypothesis that breeding body mass depends on environmental conditions during breeding, we built a General Linear Mixed effect Model (GLMM) fitted by Restricted Maximum Likelihood (REML). Only incubating and chick rearing females differed in body mass from non-breeding birds (see results below), thus only these categories were considered as breeding birds for between season comparisons of body mass. Variation in body mass was predicted by season and breeding status. We controlled for the effect of body size and moult on body mass by including wing length and moult status as predictor variables in the model. The effect of moult status on body mass variation was not significant; hence, it was dropped from the final model. We accounted for individual variability and inter-annual variation between capture years by including individual identity and year of capture in the model as random variables.

We relied on actual body mass as a proxy for body reserves because visible fat reserves are rarely observed in tropical savannah birds and pectoral muscle scores mostly vary between scores of 2 and 3. However, we are confident that body mass corrected for size is a reliable measure of relative body reserves size, even in tropical birds based on previous observations of mass gain in intra-African migrants (Nwaogu and Cresswell 2016). Prior to fitting the minimal adequate model, all GLMMs were fitted by Maximum Likelihood (ML) rather than Restricted Maximum Likelihood REML to allow comparison of models with different fixed factors using Akaike Information Criteria (AIC). Normality and homogeneity of variance were tested using the Shapiro–Wilk normality test and residual plots, respectively. The final models were then fitted with REML, which gives a better fit for models with random effects, because we were interested in modelling body mass variation at the individual level. All analyses were carried out in R version 3.1.0 (http://cran.r-project.org/package=nlme, R, Development Core Team 2015).

Results

Body mass variation at different stages of breeding

Body mass was significantly higher in incubating and brood rearing (Brood patch score 3, 4 & 5) compared to non-breeding females (Table 1, Table S2). During incubation, breeding birds were 8.1% heavier than non-breeders after controlling for body size, and inter-annual and individual variation (Table 1, Fig. 1). Body mass peaked during incubation but decreased during the brood-rearing stages (Fig. 1). The observed pattern is consistent with the assumed available foraging time at the different breeding stages (Table S1). Body mass during egg laying (Brood patch score 2) was low and this did not differ significantly from the non-breeding or post incubation stages (Fig 1). Heavier females were more likely to incubate eggs and brood chicks but this effect was more pronounced in the dry season (Fig. 2).

Body mass variation when breeding in different seasons

Difference in body mass between breeding (incubating and chick rearing) and non-breeding female birds differed significantly during the dry season (Table 2, Fig. 3). During the dry season, breeding birds were on average 5.7% heavier than non-breeding birds, after controlling for body size and inter-annual and individual variation (Table 2). Breeding birds were also on average 2.6% heavier during the dry season than in the wet season. However, in the wet season, breeding and non-breeding females did not differ in body mass (Fig. 3).

Discussion

Body mass variation in female Common bulbuls was consistent with an interrupted foraging response (Macleod and Gosler 2006). We showed that females maintained body reserves according to the likely availability of foraging time in different breeding stages (Table S1) and with seasonally dependent foraging conditions. Body mass increase was more pronounced during incubation and in the dry season, when foraging time is most limited and less food may be encountered, respectively. In the dry season, only heavy females were likely to incubate eggs or brood chicks (Fig. 2).

Body mass variation at different stages of breeding

Our results were consistent with the first hypothesis that female birds will maintain a higher body mass during incubation because time available for foraging is most restricted during incubation. Carrying body reserves may be adaptive allowing females to timetable breeding activities as a priority rather than foraging. For example, body reserves may function to keep on/off bouts minimal and sustain longer incubation duration, thus reducing nest visibility to predators by reducing activity around the nest (Basso & Richner 2015). As a consequence, the survival probabilities of incubating birds and nests may be higher because they are less likely to be predated upon (Lima 1986; Macleod & Gosler 2006; MacLeod *et al.* 2007).

Less pronounced differences between breeding stages in the wet season (Fig. 1) may result from confounding moult effects (Gosler 1994) or variation in food availability within the wet season. Moulting is largely restricted to the wet season and moulting birds may carry larger body reserves (Gosler 1994). Fluctuations in food availability peaks within the wet season due to inter-annual variation in rainfall pattern may also cause birds to vary body reserves accordingly depending on individual strategies (Cresswell 1998; Babbitt & Frederick 2008; Durant, Hjermann & Handrich 2013).

We did not find any suggestion that body mass variation was due to egg mass or increased size of reproductive organs as previously suggested for temperate birds (Redfern, 2010), which is consistent with our first hypothesis. Our results (Table 1) show clearly that the body mass of breeding female Common Bulbuls was significantly higher than non-breeding females only at the onset of incubation. This suggests that while egg-laying females may be as light as non-breeding ones, incubating or chick-rearing females (well after the egg-laying period) are not. It is unclear if the body mass variation observed during the egg phase in the wet season (Fig. 1) is (partly) due to fluctuating reproductive organ mass. The effect of mass gain due to egg or reproductive organs will likely depend on the timing of weighing, and so body mass is expected to be highly variable during the egg phase (Vezina and Williams 2003) for different individuals weighed before or after laying. Moreover, variation in body mass associated with reproductive organs may also depend on the length of the laying period and the likelihood of successive broods.

In other species male cooperation may compliment a female's foraging effort and allow more efficient foraging within restricted time (Afton 1979; Chaurand & Weimerskirch 1994; Curlee & Beissinger 1995). Males accompany females to forage during bouts between incubation, so this may improve vigilance or search efficiency for females or

both. But the role of male Bulbuls is not clear: they mate-guard females during nest building, incubation and brood rearing, and they also assist with nestling feeding, especially when females still brood nestlings, and so we might expect males to also have foraging time constraints.

Females continue brooding chicks after hatching when males feed chicks. This behaviour may be sustained by the body reserves carried during incubation, and females may lose these reserves rapidly before they take over feeding nestlings. This brooding behaviour in the absence of provisioning from their mate may explain body mass loss after incubation (Fig. 1). By brooding nestlings and losing stored body reserves, females may adapt their body mass for better flight performance during nest provisioning. This post-incubation loss of mass is similar to patterns observed in other species (Moreno 1989; Merkle and Barclay 1996; Neto & Gosler 2010). Thus, our observations suggest that the reproductive stress and flight adaptation hypotheses are not mutually exclusive and probably explain why there is no clear experimental support for each. Moreover, in temperate environments, foraging conditions during breeding may not be sufficiently unpredictable to drive significant changes in body mass between experimentally supplemented and controlled birds in normal years.

Body mass variation when breeding in different seasons

As predicted by the second hypothesis, body mass increases for incubating and brood-rearing female Common Bulbuls were more pronounced in the dry season probably due to higher starvation risk imposed by fewer foraging opportunities (Fig. 3, Table 2). We were able to rule out two potentially confounding factors. There was no indication from the seasonal population body mass pattern (Fig. S2) that predation risk varies seasonally in our study area. A difference in predation risk between the wet and the dry season should lead to a difference in population body mass average between seasons depending on the anti-predation strategy employed (see Lima 1986; Gosler, Greenwood & Perrins 1995), which we did not find. Furthermore, Common Bulbuls moult almost entirely in the wet season (Fig. S2) so that any increases in body mass during moulting should not be confounded with the observed body mass gain in the dry season.

The difference in food availability between the wet and the dry season is a fundamental assumption in this study. We believe this assumption to be reasonable because it is based on empirical observations from previous studies in the same study area (Molokwu *et al.* 2008; Molokwu *et al.* 2010; Brandt & Cresswell 2008). Furthermore, insect abundance is generally lower in the dry season as in other seasonal tropical environments (Karr 1976; Frith & Frith 1985; Arun & Vijayan 2004; Silva, Frizzas & Oliveira 2011) so that parents may work harder to raise young when they breed during the dry season. Moreover, differences in precipitation (Fig. S1) influence productivity in tropical savannah environments and for a largely frugivorous bird like the Common Bulbul, fruits are obviously less readily available in the dry season (Ting, Hartley & Burns 2008; Williams & Middleton 2008).

Our observation of higher body mass during incubation and in the dry season supports observations of higher body mass gain during breeding in species with higher survival probabilities (Cox & Cresswell 2014). Adult survival and, thus, repeat breeding may be the main determinants of fitness in the Common Bulbul because only 1 in 10 nests survive predation on average (pers. obs.). Accordingly, breeding pairs make repeated attempts to breed. In this case, selection should favour traits that enhance adult survival during breeding, therefore increasing the likelihood of future reproduction because there is a high chance that any breeding attempt will turn out unsuccessful. For example, incubating Blue Petrels *Halobaena caerulea* were found to temporarily neglect eggs once body mass fell below a threshold (Chaurand & Weimerskirch 1994). Body mass

regulation during breeding may help birds manage less favourable foraging conditions in the dry season and still invest in self-maintaining processes.

General conclusions

Intra-individual analyses of females breeding in both the wet and dry season are crucial for understanding whether this behaviour is consistent or flexible in individuals, depending on immediate foraging conditions or trade-offs that may result from other factors. We observed some level of consistency in a few individuals with breeding records between seasons but lack sufficient observations to test this; moreover, breeding records were generally few and repeated individual captures are stochastic.

Understanding body mass variation during breeding as a response to limited foraging time may provide a better appreciation of how birds manage breeding costs, depending on environmental conditions and life-history challenges. Our observations suggest that body reserves are required to buffer the consequence of restricted foraging opportunities during breeding, which may be most pronounced during incubation and in the dry season. Such mass increases during breeding are consistent with an interrupted foraging response, which also seems likely to apply to temperate birds experiencing similarly high restrictions on foraging time. This study, using capture-mark-recapture data from a West African Savannah environment also highlights the relevance of long-term bird ringing operations. It brings to light the added value of tropical seasonality, protracted breeding periods and brood patch scoring to understanding animal ecology (Redfern, 2008; Redfern, 2010).

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Table Legends

Table 1. Variation in body mass of female Common Bulbuls P*ycnonotus barbatus* between breeding stages in a tropical savannah environment. Variation in body mass was modelled by Linear Mixed-effects Model fit by Restricted Maximum Likelihood. Body mass in breeding females was compared to females with brood patch score of '0' (non-breeding females), set at the intercept in the model. Including season of capture did not improve model fit (AIC 929.55 *Vs* 929.57, L. Ratio = 1.98, p=0.16). Shapiro-Wilk normality test: W = 0.99, p-value = 0.4. Brood patch scores are explained in Table S1.

Parameters	**Estimate**	**Error**	***df***	***t***	***p***
Intercept	36.27	0.31	177	116.8	**<0.001**
Wing length	0.24	0.07	177	3.4	**0.001**
Brood patch score 1	0.60	0.79	177	0.8	0.45
Brood patch score 2	0.76	0.51	177	1.5	0.13
Brood patch score 3	2.94	0.61	177	4.8	**<0.001**
Brood patch score 4	1.81	0.68	177	2.7	**0.01**
Brood patch score 5	1.44	0.52	177	2.8	**0.01**

Random effects: Year (N=15); overall sample size = 196; sample size per brood patch score: 0 = 69, 1 = 12, 2 = 40, 3 =23, 4 = 18, 5 = 37. Significant p–values are given in bold.

Table 2. Seasonal difference in body mass of breeding and non-breeding female Common Bulbuls *Pycnonotus barbatus*, modelled by linear mixed-effects model fit by Restricted Maximum Likelihood. Breeding birds and the dry season were set at the intercept in the model. Shapiro-Wilk normality test: W = 0.99, p-value = 0.5.

Parameters	**Estimate**	**Error**	***df***	***t***	***p***
Intercept	36.30	0.32	93	112.4	**<0.001**
wing length	0.27	0.09	93	3.0	**<0.01**
Season (Wet)	0.59	0.51	93	1.1	0.25
Breeding status (breeding)	2.37	0.45	93	5.3	**<0.001**
Season : Breeding status	-1.54	0.68	93	-2.3	**0.03**

Random effects: Year and individual identity; number of individuals = 50, overall number of observations = 147. Significant p–values are given in bold.

Figure Legends
Fig. 1

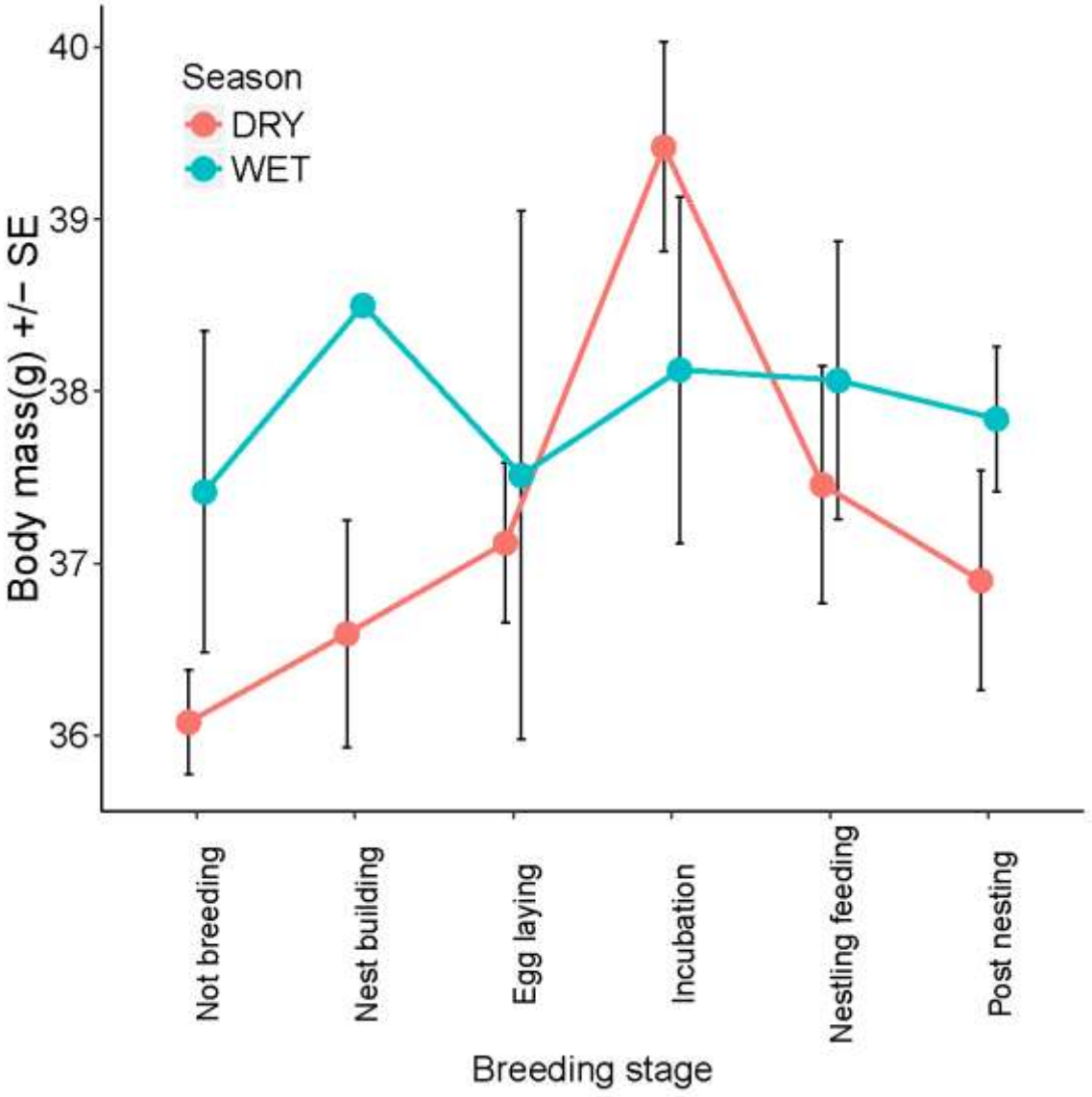

Fig. 2

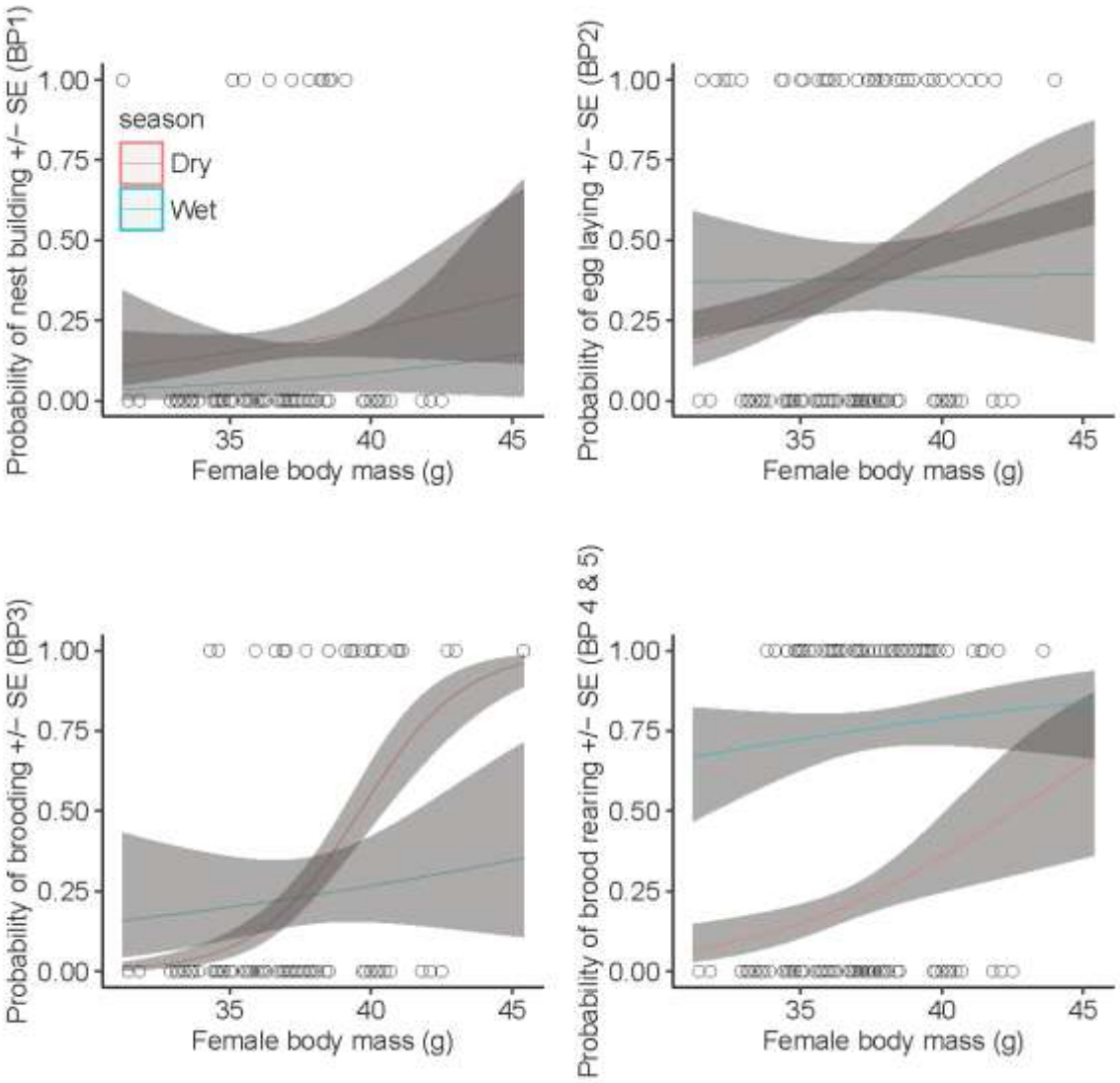

Fig. 3